

Towards a standardized characterization of the potentially migrating silver European eel (*Anguilla anguilla*, L.)

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With 3 figures and 4 tables

Abstract: We defined a standardized method for discriminating candidate silver eels that may undergo catadromous migration in the following season from the sedentary fraction of a population. A combination of two qualitative criteria (state of differentiation of the lateral line and colour contrast) and one quantitative criterion (Ocular Index OI) was used to determine the development toward silvering. In the non-migratory phase, we found a gradient of the three criteria between yellow (0 criterion), presilver (1 to 2 criteria) and silver (3 criteria) eels. In the migrant phase, silver eels had ended their metamorphosis process and were characterized at the same time by the presence of the 3 silvering criteria. A mark-recapture survey using PIT-tags provided evidence that only identified silver eels (3 silvering criteria present) in the catchment actually emigrated the following season. Moreover, the use of a single criterion of silvering among the three generated large variation in the estimated proportion of candidates for emigration which varied between -22 % and +63 %. Such a result confirmed that a multicriteria approach is needed to characterize in a standard way the potentially migrating silver eel.

Key words: yellow eel, silver eel, discrimination, multicriteria approach, silvering process, PIT-tags.

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Introduction

In the context of the major decline of Atlantic eel stocks throughout their distribution range observed since the 1980s (e.g. MORIARTY & DEKKER 1997 for European eel *Anguilla anguilla* and CASSELMAN 2003 for American eel *Anguilla rostrata*), restoration programs and local management plans have been conducted in order to restore abundance for all its inland water stages (ICES 1998). The regulation of fisheries for glass eels and/or silver eels (MORIARTY & DEKKER 1997), the management of obstructions (chemical or physical) to migration, in particular fish passes (e.g. LEGAULT 1992, KNIGHTS & WHITE 1998, FEUNTEUN et al. 1998), and restocking (MORIARTY & DEKKER 1997) are the most widely used management options (FEUNTEUN 2002).

Standardized abundance indices, based on monitoring involving many fishery managers and researchers, will be needed to assess the efficiency of such restoration plans on eel stocks. Recently, the monitoring of silver eel escape-ment has been designated as a major priority at national and European scales (LAMBERT & FEUNTEUN 1998) since it implies an assessment of the inland water dynamics of a sub-population of eels (FEUNTEUN 2002). In this context, it seems essential to identify the number and features of candidate eels ready to undertake their seaward migration in the following year, based on the analysis of a component of the sedentary population (FEUNTEUN et al. 2000).

The silvering process involves a whole series of morphological and physiological transformations that mark the transition between a sedentary growth phase (yellow eel) and a catadromous migration phase (silver eel). Numerous experiments and studies have investigated the changes that occur during the transformation from a resident yellow eel to actively migrating silver eel. They usually showed that the silvering process is a gradual phenomenon that starts in the yellow stage and that in neuro-endocrine terms consists of a succession of stages that take place from spring to autumn (FONTAINE 1994, DURIF et al. 2000). These changes are generally thought to be related to the onset of migration behaviour and gonadal development (PANKHURST 1984). Some of the metamorphic changes that have been documented in anguillid eels include increased eye diameter (PANKHURST 1982, BEULLENS et al. 1997), changes in integument structure and colour (PANKHURST & LYTHGOE 1983, FONTAINE 1994), a shift in retinal pigment sensitivity (PANKHURST & LYTHGOE 1983, PANKHURST 1984), a differentiation of the lateral line (ZACCHEI & TAVOLARO 1988), etc.

Some of these characteristics can be used to assess the migratory status of individuals eels examining one or more of these parameters (COTTRILL et al. 2002). However, despite the widespread use of morphometric variables to discriminate resident eels from migrating eels, no methodology is yet available to precisely assess the gradual evolution of silvering. Such a method is lacking

since many unclassifiable individuals that are neither completely 'yellow' nor 'silver' can be observed in the field. Thus, the fate of these eels, as candidates to seaward migration, can be questioned and is difficult to determine with a single character of silvering (FEUNTEUN et al. 2000).

The objective of our study was to define a standardized, non-destructive and rapid method adapted to field investigations to (i) specify the state of the silvering process and (ii) identify silver eels that are candidates for the seaward migration in the following season. The state of advance of metamorphosis of eels was described using a combination of three criteria representative of the sequence of observed changes during metamorphosis. Indeed, the increase of the eye diameter correlated with the higher gonad weight was the earliest change, whereas the typical pigmentation of silver eel occurred generally at the end of the process (DURIF et al. 2000, HAN et al. 2003). Thus, a quantitative criterion that expresses the ocular hypertrophy using the Pankurst Ocular Index "OI" (1982) and two qualitative criteria that specify the state of the lateral line (differentiated or not) and the colour contrast (present or not) were used. The identification of candidates to migration was based on the comparison of the combination of these criteria observed between sedentary versus migrating eels in three different sites and was validated by a mark-recapture survey using Passive Integrated Transponder (PIT) tags. Moreover, in order to show that the combination of three silvering criteria was essential for silvering eel identification, consequences of the use of a single criterion (lateral line or colour or OI) on the determination of stages were investigated.

Material and methods

Study sites

Eels were sampled in three rivers in western France: the Frémur, the Oir and the Loire. The Frémur (17 km-long) and Oir (21 km-long) are similar to a wide range of small catchments in western France as their drainage areas cover 60 km² and 87 km² respectively. The other site is located in the downstream area of the Loire (1012 km-long, the largest river in France) catchment (117500 km²).

Sedentary fish sampling

Eels were sampled in the Frémur and Oir drainages in 2002 and 2003 by electrofishing using a 'Heron' apparatus (100–500 V D. C. and 0.8–10 A; LAMARQUE et al. 1978). Sampling was conducted during the low water level period (September in the Frémur and October in the Oir), i. e. after the beginning of the metamorphosis (FONTAINE 1994) and before the effective downstream migrations of silver eels that typically begin from November in both sites with high water discharges (ACOU et al. 2000, FEUNTEUN et al. 2000).

PIT-Tagging

In Frémur, all eels > 200 mm captured by electrofishing in September 2002 were marked individually using Trovan[®] Passive Integrated Transponder (PIT) tags (dimensions: 2.12 × 11.5 mm) injected with a syringe into the abdominal cavity (PRENTICE et al. 1990). Fourteen percent of the tags were rejected one hour after the injection (ACOU 1999). Therefore, eels were kept at least an hour after tagging before they were released in the river.

Downstream migrant fish sampling

In the Frémur, a Wolf trap (6 km from the estuary) was designed to capture every descending eel > 200 mm under all flow conditions. Daily monitoring was conducted between September 2002 and September 2004. In order to identify marked eels, we used a Trovan[®] apparatus (LID500 Portable reader).

In the Loire, 13 commercial fishermen, located between 100 km and 130 km from the mouth concentrate their fishing on emigrant silver eels during river floods using a boat that supports a specific net called “guideau”. Daily monitoring was conducted during river floods in December 2002 in order to characterize the migrant eels. This net is on average 25 meters long and 8 meters wide. It is supported by two horizontal metal bars, one placed at the bottom and the other one at the surface during the fishing, and ends in a double pocket with meshing of approximately 20 mm compared to 320 mm at the entry. Fishing takes place preferably at night and lasts from 30 minutes to several hours depending on the number of captures and the obstruction of the guideau. No eel sampling was conducted in the Oir during the seaward migration period.

Each fish collected at the three different sites (Frémur, Oir, Loire) was anaesthetized with Benzocaine at a concentration of 0.15 g l⁻¹, and the total body length (TL) was measured at the nearest mm with an ichthyometer. Sex was determined by macroscopic observation of gonads, using the criteria described by COLOMBO et al. (1984) on a subsample of 45 silver eels caught in the Frémur's downstream trap. Male lengths ranged between 300 mm and 450 mm whereas all eels > 450 mm were only females as shown in other studies (TESCH 1977, ROSSI & COLOMBO 1979).

Combination of silvering criteria

Qualitative criteria

For all fish, the lateral line consists of surficial receptors (i. e. neuromasts) highly sensitive to hydrodynamic disturbances (MONTGOMERY et al. 1997). In yellow eels, these neuromasts located on the surface of the skin constitute the lateral line, and are grouped into white points of small diameter (< 1 mm)

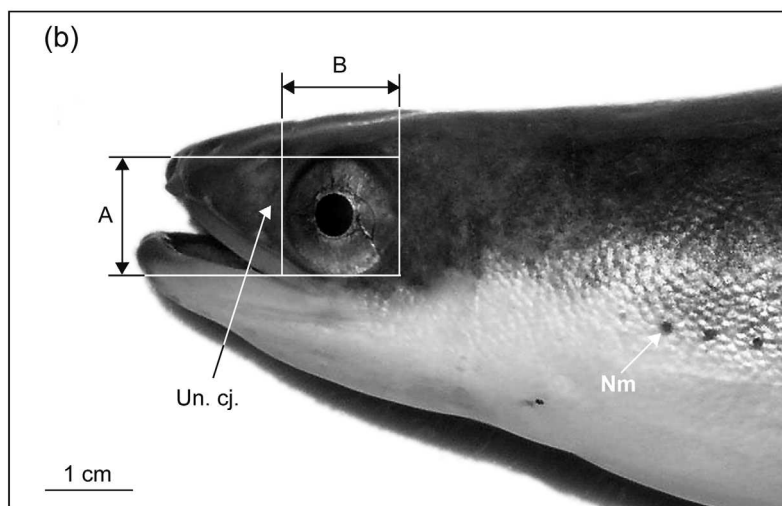
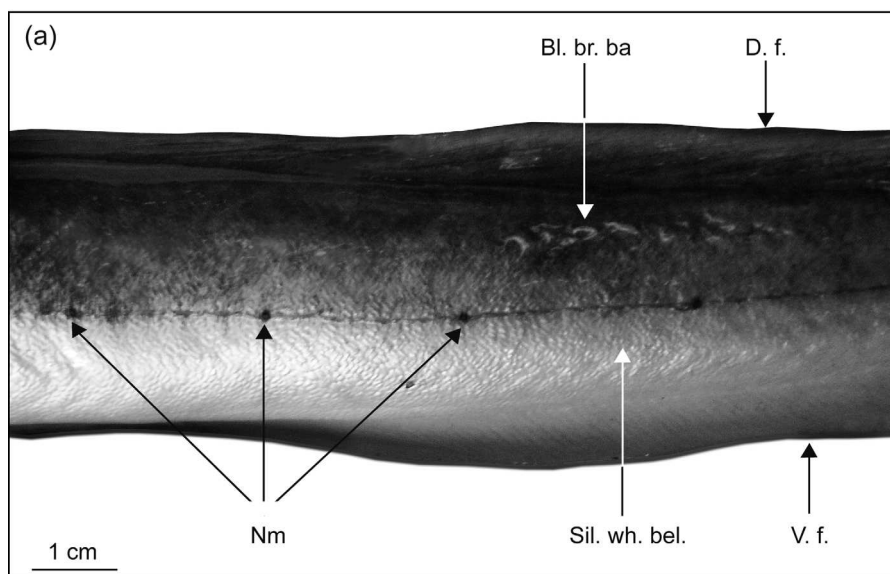


Fig. 1. (a) Body section of *A. anguilla* silver eel, showing the left profile with the differentiated lateral line composed by black corpuscles (i.e. neuromasts) and effective colour contrast between the blackish-brown back and the silvery-white belly. **(b)** Head section of *A. anguilla* silver eel showing the left eye and 4 differentiated neuromasts. D. f., dorsal fin; V. f., ventral fin; Bl. br. ba., blackish-brown back; Si. wh. bel., silvery white belly; Nm, neuromast; A, horizontal eye diameter; B, vertical eye diameter; Un. cj., unpigmented conjunctiva.

Table 1. Characteristics and coding of the criteria used to describe the silvering state of eels.

Criteria	Description	Modalities	Coding
Lateral line	Presence of at least one black corpuscle on the lateral line	True	1
		False	0
Colour contrast	Typical blackish brown back/silvery white belly	True	1
	Or		
	Significant contrast between dorsal and ventral surfaces whatever the colours (except yellow or green)	False	0
Eyes ¹	OI value	OI < 6.5	0
		6.5 ≤ OI < 8.0	1
		OI ≥ 8.0	2

¹ The OI value of 6.5 corresponds to the minimal silvering threshold value of PANKHURST (1982) defined for female eels. The OI value of 8.0 corresponds to silvering threshold value defined by MARCHELIDON et al. (1999) and ACOU et al. (2003) resulting from the analysis of female eels.

along the body. During silvering, the lateral line is clearly differentiated (ZACCHEI & TAVOLARO 1988). Visual observations in the field indicate that the white points, which are gradually surrounded by a black circle, increase in diameter to finally become black bodies of a diameter varying from 1 to 2 mm (Fig. 1). They form a distinct and continuous line along the body from the base of the pectoral fin to the tail (VOIGT et al. 2000). They are located 1 to 2 cm apart, and their numbers vary between 5 and 30 according to the size and the maturity of the eel (A. ACOU, personal observation).

The typical silver eel has a dark dorsal surface and a white ventral surface with metallic reflections, both zones being generally delimited by the lateral line (Fig. 1). The evaluation of the colour of an eel is subjective (PANKHURST 1982) and does not constitute a relevant criterion for determining the different stages of eels (PANKHURST & LYTHGOE 1983). The changes in the colour of eel skin are often variable, since they are not only dependent on the degree of maturity but also on growth habitat and adaptation of eel to its habitat (TESCH 1977). The relative contrast observed between ventral and dorsal surface, generally well-marked in silver individuals, is a more objective criterion which disregards colorimetry (Table 1). However, both ventral and dorsal surfaces in silver eels can be quite variable in hue and intensity. We therefore considered in this study that the colour contrast used for our classification could be (i) the typical blackish-brown back/silvery-white belly or (ii) a significant contrast between dorsal and ventral surface whatever the colours (with the exception of yellow and green coloration) (Table 1).

Thus, the clear differentiation of the lateral line, based on the presence of the black corpuscles, and the changes in skin colour, represented by the contrast of colours between the dorsal and ventral surfaces, are two objective qualitative criteria to be tested in our study in order to accurately determine the degree of silvering (Table 1).

Quantitative criterion

The ocular index (OI), defined as the relation between the total length of the eel and the mean size of the two eyes, was calculated using the following formula (PANKHURST 1982):

$$OI = \{((A_R + B_R)/4) \times ((A_L + B_L)/4) \times \pi/TL\} \times 100$$

where A and B are the horizontal and vertical eye diameters, respectively, TL is the total body length and R and L are the diameters of the right and left eyes. Measurement of horizontal and vertical eye diameters are made from the margins formed by the pigmented area adjacent to the unpigmented conjunctiva (Fig. 1). In this study, vertical and horizontal eye diameters were measured for both eyes in order to limit OI error imprecision. Measurements of total length were made with an ichthyometer (i.e. a ruler fixed in the bottom of a gutter) to the nearest mm. Measurements of eye diameters were made with a standard calliper to the nearest 0.02 mm. Length and OI data presented are means \pm Standard Deviation (S.D.).

Three classes of OI defined from the threshold values at silvering of 6.5 (PANKHURST 1982) and 8.0 (MARCHELIDON et al. 1999, ACOU et al. 2003) characterize the ocular hypertrophy observed during metamorphosis (Table 1). Thus, each eel was described by the combination of the three categorical criteria in this order: clear differentiation of the lateral line (0 or 1), colour contrast of the skin (0 or 1) and OI class (0, 1 or 2) (Table 1).

Results

Sedentary fraction

214 and 149 eels were sampled by electrofishing in the Frémur and in the Oir, respectively. They were ranked according to the presence of the three silvering criteria (lateral line, skin colour, OI class) (Table 2). Eels that did not have any silvering criterion were the most abundant: 72.9 % (N = 156) and 91.3 % (N = 136) of total catches in the Frémur and Oir, respectively. Eels with the three criteria (combinations 1–1–1 and 1–1–2) represented 12.6 % (N = 27) and 6 % (N = 9) of total catches. In the Oir, no eel had a single criterion and eels with two criteria only represented 2.7 % (N = 4) of all individuals. In the Frémur,

Table 2. Description of the combinations of silvering criteria observed for (i) sedentary eels caught by electrofishing in the Frémur and the Oir and (ii) migrant eels (descending) caught during downstream migration peaks in the Frémur and in the Loire. The combinations are the qualitative silvering criteria in the following order (1) clearly differentiated lateral line and (2) contrasting colour between dorsal and ventral surfaces, and (3) a quantitative criterion characterizing ocular hypertrophy compared to the OI threshold values (cf. Table 1 for the coding of the 3 criteria).

Number of silvering criteria observed	Combination	Sedentary		Migrant	
		Frémur	Oir	Frémur	Loire
0	0-0-0	156	136	8	0
1	0-0-1	7	0	0	0
	0-0-2	1	0	0	0
	0-1-0	3	0	0	0
	1-0-0	8	0	0	0
	<i>total</i>	<i>19</i>	<i>0</i>	<i>0</i>	<i>0</i>
2	0-1-1	1	0	0	0
	0-1-2	2	0	0	0
	1-0-1	2	0	0	0
	1-0-2	2	0	0	0
	1-1-0	5	4	4	2
	<i>total</i>	<i>12</i>	<i>4</i>	<i>4</i>	<i>2</i>
3	1-1-1	7	2	42	13
	1-1-2	20	7	319	138
	<i>total</i>	<i>27</i>	<i>9</i>	<i>361</i>	<i>151</i>
	<i>Total</i>	<i>214</i>	<i>149</i>	<i>373</i>	<i>153</i>

8.9 % (N = 19) and 7.7 % (N = 12) of sampled eels had 1 and 2 cumulated criteria, respectively.

Migrant fraction

General characteristics

373 and 153 individuals were caught in the Frémur trap and in the Loire, respectively (Table 2). In the Frémur, female silver eels represented 55.7 % (N = 208) of the total catch. In the Loire, all eels sampled were females. The mean length of female silver eels in the Frémur (589.5 ± 97 mm) was significantly lower than in the Loire (765.8 ± 85 mm) [One-Way ANOVA, F(1,349) = 311.2, p <0.001].

Combination of criteria

96.8 % (N = 361) and 98.7 % (N = 151) of emigrant eels trapped had a differentiated lateral line, a contrasting colour and an OI value higher than the thresh-

Table 3. Number of eels marked by Passive Integrated Transponder (PIT)-tags following electrofishing (EF) in autumn 2002 in the Frémur and subsequent recaptures either in the downstream trap (trap) or in the catchment (EF) in autumn 2003.

Tagging		Recapture				
No. of silvering Criteria observed	EF Autumn 2002	Trap 2002 3 silvering criteria	EF Autumn 2003: No. of silvering criteria			Total
			0	1 or 2	3	
0	55	0	11	1	4	16
1 or 2	12	1	0	0	0	1
3	23	7	0	0	0	7
Total	111	8	11	1	4	24

hold value of 6.5 (combinations 1–1–1 and 1–1–2) in the Frémur and the Loire, respectively (Table 2). Among them, 88.4 % (N = 319) and 91.4 % (N = 138) had an OI ≥ 8.0 (combination 1–1–2) in the two sites, respectively. The mean OI of eels with the combinations 1–1–1 and 1–1–2 were 7.42 ± 0.39 and 10.16 ± 1.40 in the Frémur and 7.35 ± 0.42 and 10.30 ± 1.27 in the Loire. The 6.5 OI value appeared to be an accurate threshold value since only 1.1 % and 1.3 % of emigrant eels had only two silvering criteria (combination 1–1–0) in the Frémur and Loire, respectively. No migrant eels at either sampling site had only one silvering criterion. Lastly, 2.1 % (N = 8) of eels trapped in the Frémur were characterized by the combination 0–0–0 with a mean OI of 4.64 ± 0.98 , whereas no eel was found with this combination in the Loire.

PIT-tagging survey

111 eels sampled by electrofishing in autumn 2002 in the Frémur were individually tagged (Table 3). Among them, 55 individuals were yellow eels (combination 0–0–0). None were recaptured in the following season as emigrant silver eel in the downstream trap, and 29.1 % (N = 16) were recaptured in the catchment in autumn 2003 as yellow eel (N = 11), presilver eel (N = 1) and silver eels (N = 4).

Among the 12 eels tagged in autumn 2002 that showed between 1 and 2 silvering criteria, only 1 eel (combination 1–1–0) was recaptured in the downstream trap in 2002 as silver eel (combination 1–1–2). However, the difference of OI variation (coefficient of variation c. v.: 23.7 %) of this individual between the sedentary (combination 1–1–0) and the migrant phase (1–1–2) compared with the mean variation in silver eels during the same period (mean c. v.: 5 %, N = 7) suggested an error measurement of ocular diameters. This individual was therefore *a posteriori* reclassified as silver eel in the sedentary fraction.

Table 4. Differences expressed as percentage between numbers of silver eels defined according to the combination of the 3 silvering criteria present (combination reference 111; see Table 2 for reference number calculation) and those estimated by each criterion taken individually (in %). The number of eels is given in brackets.

Fractions	Sites	Reference number of silver eels	Differentiated lateral line	Contrasted colour	Ocular Index	
					≥ 6.5	≥ 8.0
Migrant	Frémur	361	+1 (365)	+1 (365)	0 (361)	-12 (319)
	Loire	151	+1 (153)	+1 (153)	0 (151)	-9 (138)
Sedentary	Frémur	27	+63 (44)	+41 (38)	+56 (42)	-7 (25)
	Oir	9	+44 (13)	+44 (13)	0 (9)	-22 (7)

Indeed, among the 23 eels tagged that presented three silvering criteria (combinations 1-1-1 and 1-1-2), 8 were found in the downstream trap in 2002 (Table 3). In other words, 34.8 % of the potentially emigrant silver eels present in the catchment actually emigrated during the following migration season. The remaining silver eels were neither recaptured in the catchment in autumn 2003 nor in the trap in 2003.

Comparisons of silvering criteria within both life stages

Emigrant silver eels were characterized by a minimum reference combination corresponding to 1-1-1 (Table 2). If the identification of the stages was based on using only one criterion among the three (differentiated lateral line or contrasting colour or OI value higher than the threshold values of 6.5) this led to large variations in the estimated proportion of potentially silver eels compared to our minimum silver eel reference (combination 1-1-1, Table 4). For eels sampled in the sedentary phase, the variations observed were very large since they varied between -7 % and +63 % in the Frémur and -22 % and +44 % in the Oir (Table 4). Using the differentiated lateral line or the contrasting colour as a single silvering criterion led to an average overestimation of 50 % in the proportion of the potentially silver eels in both sites.

In the Frémur, we observed a positive and significant correlation between OI and TL values of eels having between 0 and 2 criteria of silvering (Pearson $r = 0.62$, $p < 0.05$, $N = 182$; Fig. 2). According to our silver reference, the yellow eels (0 criteria present) and/or eels in the process of silvering (1 to 2 criteria present) were not expected to be “emigration candidates” in the following season. However, among these eels in the process of silvering (1 to 2 criteria present), 48.4 % ($N = 15$) and 16.1 % ($N = 5$) had an OI higher than the threshold values of 6.5 and 8.0, respectively. As a consequence, the use of OI threshold values as a single criterion for silvering led to poor classification. First, the use of 6.5 threshold value led to overestimation (+56 %; Table 4) because

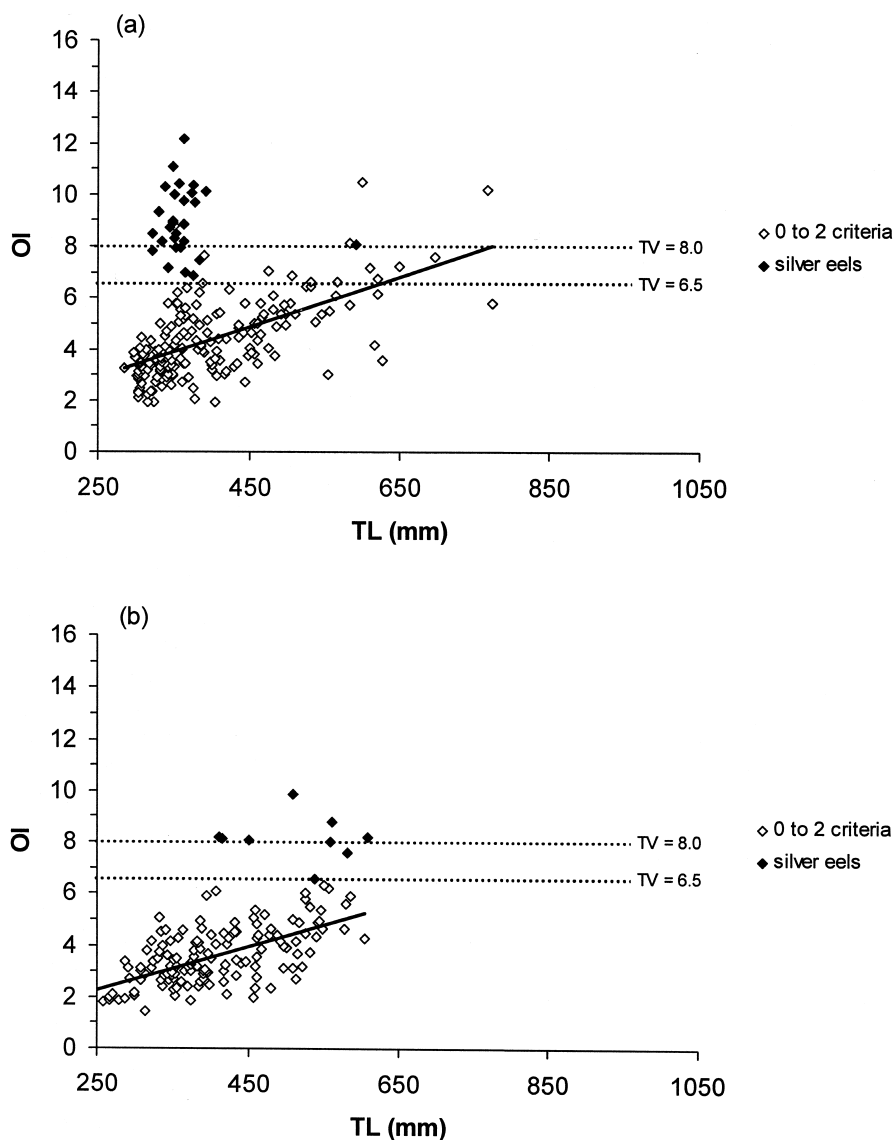


Fig. 2. Relation between the Ocular Index (OI) and body length (TL) for eels having between 0 and 2 silvering criteria and silver eels (silver combination reference 111) in catchments of (a) Frémur and (b) Oir. Significant correlations were observed for eels ($p < 0.001$). OI threshold values (TV) are indicated.

all emigration candidates as well as eels in progress of silvering were selected. Second, the use of any other threshold value > 6.5 (7.0, 7.5 for example) lead to underestimation because part of the 'real' emigration candidates were ex-

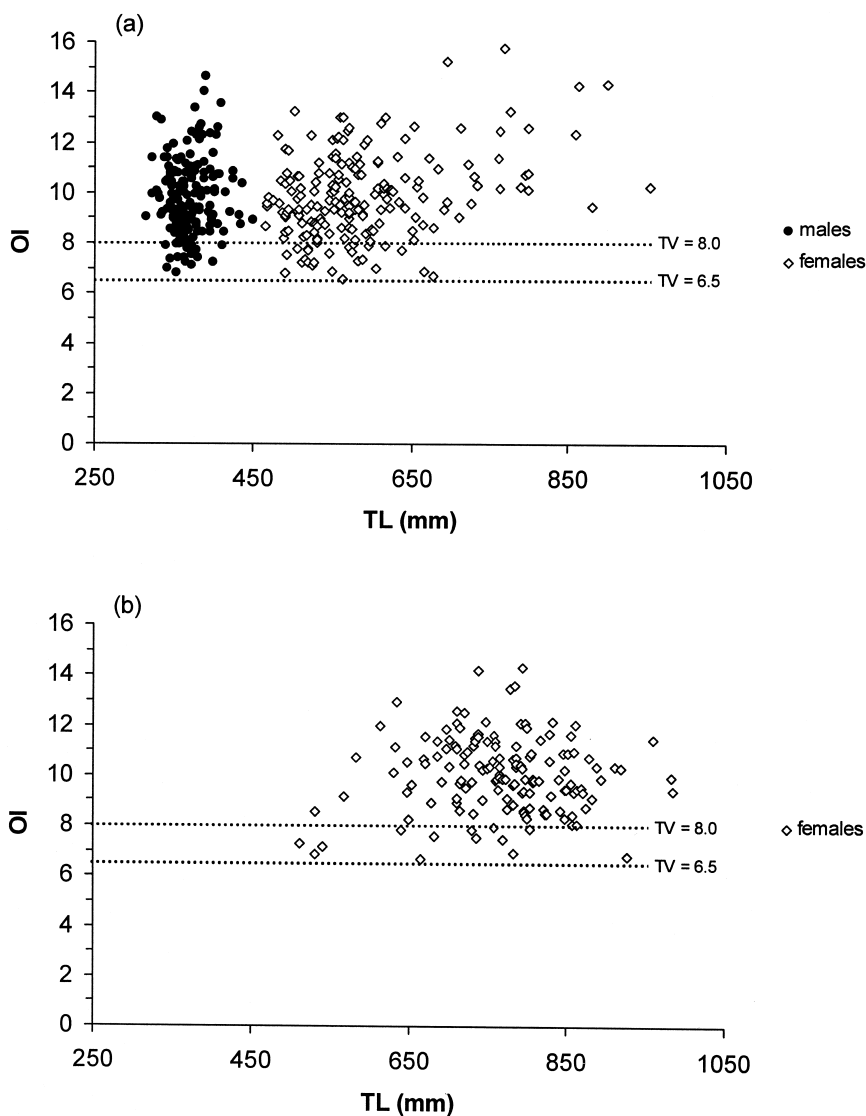


Fig. 3. Relation between Ocular Index (OI) and body length (TL) for emigrant silver eels (silver combination reference 1–1–1), for each sex, sampled in downstream migration in catchments of (a) Frémur and (b) Loire. No significant correlations are observed. OI threshold values (TV) are indicated.

cluded of the classification whereas some eels in the process of silvering could also be selected (–7 % for OI threshold value 8.0 for example; Table 4) because of the positive linear relation between OI and TL in yellow eels and eels in progress of silvering (Fig. 2).

In the Oir, we also observed a positive and significant correlation between TL and OI values in eels showing 0 to 2 criteria of silvering (Pearson $r = 0.61$, $p < 0.05$, $N = 136$; Fig. 2). However, the low number of eels characterized by the presence of 1 and 2 criteria of silvering ($N = 4$) resulted in there being no difference between silver eels defined by the 1–1–1 combination and the OI threshold value of 6.5. Lastly, the threshold value of 8.0 led to an underestimation in the proportion of silver eels of -22% (Table 4).

For eels sampled in the migrant phase, we recorded a negligible variation in the proportions of silver eels defined with the 1–1–1 reference combination and the use of the lateral line, colour or OI threshold value silvering criteria on their own ($\leq 1\%$ of overestimation) (Table 4; Fig. 3). The use of the OI threshold value of 8.0 led to an underestimation in the proportions of emigrant silver eels of -12% and -9% in the Frémur and Loire, respectively (Table 4; Fig. 3).

Discussion

Our method, which aims at quickly identifying in the field a silver eel ready to migrate, in a standard way and without sacrificing fish, is based on the analysis of three standard macroscopic criteria which constitute adaptations to migration in the deep sea. At the term of their continental phase, the silver eel Gonado-Somatic Index does never exceed 2% (FONTAINE 1994, MARCHELIDON et al. 1999, ACOU et al. 2003) whereas it can attain 80% under experimental conditions simulating hydrostatic pressure conditions of the Sargasso Sea spawning site (DUFOUR 1994). Thus, silver eels are not able to reproduce at the end of their life in fresh waters, and they can be said to be “subadult” individuals that have already undergone a series of adaptations. The significant increase of in eye diameter observed during metamorphosis is accompanied with a number of changes in the retina including a decrease in the density of cones (PANKHURST & LYTGOE 1983) consistent with the condition of the retinae of deep-sea fish in which cones are often absent. The clear differentiation of the lateral line observed during silvering is also a fundamental adaptation for the transoceanic migration. The lateral line is a mechanosensorial organ sensitive to currents permitting eels to perceive their close environment through predator avoidance (BLAXTER & FUIMAN 1989), obstacle avoidance (HASSAN 1989) and rheotaxis (MONTGOMERY et al. 1997, MONTGOMERY et al. 2000). During metamorphosis, this organ becomes well-pigmented and very visible as a result of an increase in the number of neuromasts (ZACCHEI & TAVOLARO 1988). In the same way, the capacity to increase the contrast between dorsal and ventral coloration, typical of pelagic organisms, provide an effi-

cient camouflage, which increases their chance of survival (DENTON & NICOL 1966).

Analyses of eels sampled in the sedentary phase in the Frémur and Oir watersheds have shown that the combination of the presence/absence of the three macroscopic criteria of silvering, provided a discrimination of the state of progress of this metamorphosis. We clearly distinguished a gradient of present criteria between yellow eels (0 criterion observed) and silver eels (3 criteria present), whereas a relatively large number of eels had between 1 and 2 silvering criteria. Almost 14.5 % of eels caught in the Frémur showed between 1 (8.9 %) and 2 (5.6 %) silvering criteria. These eels, which can be assumed to be in the process of metamorphosis, only accounted for 2.7 % of the total catch in the Oir watershed. Acquisition of ocular hypertrophy ($OI \geq 6.5$) as well as the differentiation of the lateral line in the Frémur, were the earliest signs of silvering since they each identified 42 % of eels having a sole silvering criterion, the contrasting colour appearing later. These results confirmed the conclusion of DURIF et al. (2000, 2005) who emphasized a succession of internal and external changes during the metamorphosis. In particular, they showed that the increase of the ocular diameter, correlated with the higher gonad weight, were the earliest changes, whereas the typical pigmentation of silver eel occurred generally at the end of the process. Therefore, our method allows an eel to be placed in a sequence of observed changes during metamorphosis. Nevertheless, the time required for an eel to complete metamorphosis remains unknown (COTTRILL et al. 2002). Such information is fundamental if we want to precisely determine those individuals that will migrate in the following season among eels in the process of silvering. In our study, the sampling was conducted in September/October in both sites, when most silvering eels had already finished their metamorphosis (TESCH 1977, FONTAINE 1994). Moreover, PIT-tagging results confirmed that neither yellow nor presilver eels actually emigrated as silver eels in the following season.

Analyses of migrant eels caught in the Frémur and the Loire during the seaward peak migration confirmed that metamorphosis does not proceed further in freshwater. Our results clearly showed that >97 % of emigrant silver eels were characterized by a differentiated lateral line, a contrasting color and an $OI \geq 6.5$ as defined by PANKHURST (1982) (combinations 1–1–1 and 1–1–2).

A very low proportion of eels (<1.5 %) observed in the Frémur and Loire samples presented the combination 1–1–0. Considering the sequence of appearance of metamorphic characteristics during silvering, those eels may have an underestimated OI value. Indeed, OI implies the measurement of 5 variables (TL and eyes diameters) in a formula which can be sensitive to measurement error. A comparative study using 13 European eels and 3 replicated measurements by three different observers showed that the estimated amplitude of OI imprecision at 95 % confidence level was 1.8 whatever eel length

and observer (ACOU, unpubl. data). However, we assumed in this study that the combination 1–1–0 did not characterize a potentially silver eel that would migrate in the following season.

PIT-tagging survey provided evidence that only silver eels identified from their external appearance (1–1–1 or 1–1–2) in the catchment actually emigrated the following season. However, the recapture rate observed between the sedentary and the migratory fraction was rather low (34.8 %) and, therefore, the fate of the remaining identified silver eels (64.2 %) that were not recaptured is unknown. Our sampling effort allowed the recapture of tagged yellow eels (combination 0–0–0) in the following year confirming the sedentary lifestyle of this stage in inland freshwaters (LAFFAILLE et al. 2005). In contrast, no identified silver eels tagged in autumn 2002 were recaptured the following year in the catchment suggesting that they at least moved away from their initial tagging site. Several hypotheses can be postulated. First, eels may escape from the downstream trap during migration. Secondly, natural mortality (about 5–10 % year⁻¹, e. g., ADAM 1997), fishing pressure (no professional fishery but many anglers) or predation might have reduced the tagged population. Thirdly, a major obstruction located between the stations sampled by electrofishing and the downstream trap may alter downstream migration dynamics of silver eels. It is 14-m high and creates a reservoir to provide the county with drinking water. Most of the time, it is not full and the flow is controlled by pipes. During the period of downstream migration, the influence of classical environmental parameters (e. g., river discharge, rainfall) that triggered emigration intensity was overruled by dam management. Emigration was impossible until the reservoir was full and overflowing water permitted eels to slide down the weir (see FEUNTEUN et al. 2000 for further details) which caused an important delay of migration compared to a non-obstructed river and/or stop of the run (ACOU et al. 2000, VOLLESTAD et al. 1986). Indeed, an eel that has missed the favourable ‘environmental windows’ can possibly stop its catadromous migration and revert back to the growth phase (DURIF et al. 2003, 2005). An extra sampling campaign in the reservoir should enable us to better understand the fate of these eels.

Our results further showed the need to use a multicriteria approach for estimating potentially silver eels. Indeed, the use of a sole silvering criterion among the three led to great differences in the estimated proportions of silver eels in comparison with our silver eel reference (combination 1–1–1). These variations are related to the fact that the use of a single criterion (i) cannot be used to position an individual in the metamorphic sequence observed during silvering and (ii) emphasizes the inherent skew due to the use of this criterion.

The most meaningful example is indisputably the use of OI the threshold values 6.5 (PANKHURST 1982) and 8.0 (MARCHELIDON et al. 1999, ACOU et al. 2003), which led to an overestimation of 56 % and an underestimation of 22 %

of the potentially emigrating eels, respectively. Because of the imprecision in the calculation of OI and the fact that ocular hypertrophy appears to be among the first metamorphic changes (DURIF et al. 2000, HAN et al. 2003), identifying silvering solely on the basis of OI threshold values thus poses problems since sampled eels have OI values that are close to these boundaries. Moreover, as the increase in OI is a gradual phenomenon that starts at the yellow eel stage (MARCHELIDON et al. 1999), large overlaps may occur between eels at the OI threshold values during sampling of a “sedentary” population fraction in late summer or in autumn, whatever the eel stages are. This was confirmed by COTTRILL et al. (2002) for female American silver eel *A. rostrata*. The relevance of our method depends on the combination of the three silvering criteria. We therefore recommend the use of the criteria defined in this study in order to precisely assess the proportion of potentially emigrating eels among a sedentary population fraction, i.e. we consider that a silver eel ready to migrate in the following season is characterized by a differentiated lateral line, a contrasting colour and an $OI \geq 6.5$.

Silvering dynamics probably vary according to the ecological subunits (catchments, lagoon, etc.), habitat index and geographic situation, since such variables are known to influence the sex ratio, population structure, and population size (FEUNTEUN et al. 2000). Length and age at silvering for European eel are known to vary greatly between and within ecological units (DE LEO & GATTO 1995, VOLLESTAD 1992, ACOU et al. 2003). The standardized identification of potentially silver migrant eels constitutes a fundamental step in order to analyse and model the life history traits of the European eel (age and size at silvering notably) at the scale of its distribution range. Moreover, this method should permit also to better understand the migratory dynamics of silver eels according to the degree of river regulation that may alter the natural flow regimes. This approach is thus required to start reliable management of this panmictic species, which is considered outside safe biological limits (ICES 1998).

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References

- ACOU, A. (1999): L'anguille européenne, dynamique et déterminisme de la migration catadrome dans un bassin versant anthropisé de Bretagne (Frémur). – Diplôme doctoral de l'Université de Rennes 1, 167 p.
- ACOU, A., FEUNTEUN, E., LAFFAILLE, P. & LEGAULT, A. (2000): Catadromous migration dynamics of European Eel (*Anguilla anguilla* L.) in a dammed catchment. – Verh. Internat. Verein. Limnol. **27**: 1–4.
- ACOU, A., LEFEBVRE, F., CONTOURNET, P., POIZAT, G., PANFILI, J. & CRIVELLI, A. J. (2003): Silvering of females eels (*Anguilla anguilla*) in two sub-populations of the Rhône Delta. – Bull. Fr. Pêche Piscic. **368**: 55–68.
- ADAM, G. (1997): L'anguille européenne (*Anguilla anguilla* L. 1758): dynamique de la sous population du lac de Grand-Lieu en relation avec les facteurs environnementaux et anthropiques. – Thèse Univ. de Toulouse 3, 299 p.
- BEULLENS, K., EDING, E. H., OLLEVIER, F., KOMEN, J. & RICHTER, C. J. J. (1997): Sex differentiation, changes in length, weight and eye size before and after metamorphosis of the European eel (*Anguilla anguilla* L.) maintained in captivity. – Aquaculture **153**: 151–162.
- BLAXTER, J. H. S. & FUIMAN, L. A. (1989): Function of the free neuromasts of marine teleost larvae. – In: COOMBS, S., GÖRNER, P. & MÜNZ, H. (eds): The Mechanosensory Lateral Line. Neurobiology and Evolution. – Springer-Verlag, New York, pp. 481–499.
- CASSELMAN, J. M. (2003): Dynamics of resources of the American eel, *Anguilla rostrata*: Declining abundance in the 1990's. – In: AIDA, K., TSUKAMOTO, K. & YAMAUCHI, K. (eds): Tokyo Eel Biology. – Springer-Verlag, New York, pp. 255–274.
- COLOMBO, G., GRANDI, G. & ROSSI, R. (1984): Gonad differentiation and body growth in *Anguilla anguilla*, L. – J. Fish Biol. **24**: 215–228.
- COTTRILL, R. A., MCKINLEY, R. S. & VAN DER KRAAK, G. (2002): An examination of utilizing external measures to identify sexually maturing female American eels, *Anguilla rostrata*, in the St. Lawrence River. – Envir. Biol. Fishes **65**: 271–287.
- DE LEO, G. A. & GATTO, M. (1995): A size and age-structured model of the European eel (*Anguilla anguilla* L.). – Can. J. Fish. Aquat. Sci. **52**: 1351–1367.
- DENTON, E. J. & NICOL, J. A. C. (1966): A survey of reflectivity in silvery teleosts. – J. Mar. Biol. Assoc. UK, **46**: 685–672.
- DUFOUR, S. (1994): Neuroendocrinologie de la reproduction de l'anguille: de la recherche fondamentale aux problèmes appliqués. – Bull. Fr. Pêche Pisc. **335**: 187–211.
- DURIF, C., DUFOUR, S. & ELIE, P. (2005): The silvering process of *Anguilla anguilla*: a new classification from the yellow resident to the silver migrating stage. – J. Fish Biol. **66**: 1025–1043.
- DURIF, C., ELIE, P., DUFOUR, S., MARCHELIDON, J. & VIDAL, B. (2000): Analysis of morphological and physiological parameters during the silvering process of the European eel (*Anguilla anguilla*) in the Lake of Grand-Lieu (France). – Cybium, **24**(Suppl. 3): 63–74.
- DURIF, C., GOSSET, C., RIVES, J., TRAVADE, F. & ELIE, P. (2003): Behavioral study of downstream migrating eels by radio-telemetry at a small hydroelectric power plant. – In: DIXON, D. A. (ed.): *Biology, Management and Protection of Catadromous Eels*. – Bethesda, MD: American Fisheries Society, Symposium 33, pp. 343–356.

- FEUNTEUN, E. (2002): Management and restoration of European eel population (*Anguilla anguilla*): An impossible bargain. – Ecol. Eng. **18**: 575–591.
- FEUNTEUN, E., ACOU, A., GUILLOUËT, J., LAFFAILLE, P. & LEGAULT, A. (1998): Spatial distribution of an eel population (*Anguilla anguilla* L.) in a small coastal catchment of Northern Brittany (France). Consequences of hydraulic works. – Bull. Fr. Pêche Piscic. **349**: 129–139.
- FEUNTEUN, E., ACOU, A., LAFFAILLE, P. & LEGAULT, A. (2000): European eel (*Anguilla anguilla*): prediction of spawner escapement from continental population parameters. – Can. J. Fish. Aquat. Sci. **57**: 1627–1635.
- FONTAINE, Y. A. (1994): L'argenture de l'anguille: métamorphose, anticipation, adaptation. – Bull. Fr. Pêche Piscic. **335**: 171–185.
- HAN, Y.-S., LIAO, I.-C., HUANG, Y.-S., HE, J.-T., CHANG C.-W. & TZENG, W.-N. (2003): Synchronous changes of morphology and gonadal development of silvering Japanese eel *Anguilla japonica*. – Aquaculture **219**: 783–796.
- HASSAN, E. S. (1989): Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish *Anoptichthys jordani*. – In: COOMBS, S., GÖRNER, P. & MÜNZ, H. (eds): The Mechanosensory Lateral Line. Neurobiology and Evolution. – Springer-Verlag, New York, pp. 217–228.
- ICES (1998): European eel. – Extract of report of the Advisory Committee on Fishery Management, No. 11. ICES, Copenhagen, Denmark.
- KNIGHTS, B. & WHITE, E. (1998): Enhancing immigration and recruitment of eels: the use of passes and associated trapping systems. – Fisheries Managem. Ecol. **5**: 459–471.
- LAFFAILLE, P., ACOU, A. & GUILLOUËT, J. (2005): The yellow European eel (*Anguilla anguilla* L.) may adopt a sedentary lifestyle in inland freshwaters. – Ecol. Fresh. Fish. **14**: 191–196.
- LAMARQUE, P. J., ARIGNON, J. & GOSSET, C. (1978): Comparaison des appareils de pêche à l'électricité EPMC et héron. – Bull. Fr. Pêche Piscic. **270**: 223–236.
- LAMBERT, P. & FEUNTEUN, E. (1998): Compte rendu des journées anguilles de Paimpont du 23 au 25 Septembre 1998. – Rapport GRISAM, Cemagref Bordeaux, University Rennes 1, France.
- LEGAULT, A. (1992): Etude de quelques facteurs de sélectivité des passes à anguilles. – Bull. Fr. Pêche Piscic. **325**: 83–91.
- MARCHELIDON, J., LE BELLE, N., HARDY, A., VIDAL, B., SBAIHI, M., BURZAWA-GERARD, E., SCHMITZ, M. & DUFOUR, S. (1999): Etude des variations de paramètres anatomiques et endocriniens chez l'anguille européenne (*Anguilla anguilla*) femelle, sédentaire et d'avalaison: Application à la caractérisation du stade argenté. – Bull. Fr. Pêche Piscic. **355**: 349–368.
- MONTGOMERY, J. C., BAKER, C. F. & CARTON, A. G. (1997): The lateral line can mediate rheotaxis in fish. – Nature **389**: 960–963.
- MONTGOMERY, J. C., CARTON, G., VOIGT, R., BAKER, C. & DIEBEL, C. (2000): Sensory processing of water currents by fishes. – Phil. Trans. R. Soc. Lond. **B 355**: 1325–1327.
- MORIARTY, C. & DEKKER, W. (Editors) (1997): Management of European eel fisheries. – Ir. Fish. Bull. No. 15.
- PANKHURST, N. W. (1982): Relation of visual changes to the onset of sexual maturation in the European eel *Anguilla anguilla* (L.). – J. Fish Biol. **21**: 127–140.

- (1984): Artificial maturation as a technique for investigating adaptations for migration in the European eel, *Anguilla anguilla* (L.). – In: MCLEAVE, J. D., ARNOLD, G., DODSON, J. & NEILL, W. (eds): Mechanisms of Migration in Fishes. – NATO Scientific Affairs Division, New York, pp. 143–157.
- PANKHURST, N. W. & LYTGOE, J. N. (1983): Changes in vision and olfaction during sexual maturation in the European eel *Anguilla anguilla* (L.). – J. Fish Biol. **23**: 229–240.
- PRENTICE, E. F., FLAGGS, T. A. & CUTCHEON, M. C. (1990): Electronic tag. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. – Amer. Fish. Soc. Symp. **7**: 317–322.
- ROSSI, R. & COLOMBO, G. (1979): Some observations on age, sex, growth of silver eels (*Anguilla anguilla* L.) in north Adriatic Lagoons. – Rapp. P.-v. Réunion. Cons. Int. Explor. Mer. **174**: 64–69.
- TESCH, F. W. (1977): The eel. Biology and management of anguillid eels. – Chapman and Hall, London, U. K.
- VOIGT, R., CARTON, A. G. & MONTGOMERY, J. C. (2000): Response of anterior lateral line afferent neurones to water flow. – J. Exp. Biol. **203**: 2495–2502.
- VOLLESTAD, L. A. (1992): Geographical variation in age and length at metamorphosis of maturing European eels: environmental effects and phenotypic plasticity. – J. Anim. Ecol. **61**: 41–48.
- VOLLESTAD, L. A., JONSSON, B., HVIDSTEN, N. A., NAESJE, T. F., HARALDSTAD, O. & RUUD-HANSEN, J. (1986): Environmental factors regulating the seaward migration of silver eels (*Anguilla anguilla*). – Can. J. Fish Aquat. Sci. **43**: 1909–1916.
- ZACCHEI, A. M. & TAVOLARO, P. (1988): Lateral line system during the life cycle of *Anguilla anguilla* L. – Boll. Zool. **3**: 145–153.